Implications of mechanistic modeling of drought effects on growth and competition in forest landscape models

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Abstract. The incidence of drought is expected to increase worldwide as a factor structuring forested landscapes. Ecophysiological mechanisms are being added to Forest Landscape Models (FLMs) to increase their robustness to the novel environmental conditions of the future (including drought), but their behavior has not been evaluated for mixed temperate forests. We evaluated such an approach by assessing the ability of physiological mechanisms to predict susceptibility to tree mortality as a function of drought in the upper Midwest (USA) through controlled site-level drought simulation experiments using the PnET-Succession extension of the LANDIS-II FLM. We also conducted a landscape-level experiment to study landscape response to drought treatments in the presence of the spatial processes of seed dispersal and stand-replacing disturbance. At the site level we found that net photosynthesis and carbon reserves showed a clear negative response to both the length of drought and the alternating pulses of normal precipitation and drought events, with soils holding more water moderating this response. The effect of the drought treatments varied somewhat depending on the assemblage of competitors and their specific life-history traits such as ability to compete for light, maximum photosynthetic capacity and water use efficiency. A large diversity of assemblages were simulated at the landscape level, and species abundance generally sorted by photosynthetic capacity (foliar nitrogen) and life form (deciduous vs. evergreen), with faster growing species and deciduous species suffering less decline because of drought. Soil type also had an impact on total productivity (biomass), with soils having higher available water being more productive through time. We conclude that (1) the mechanistic, first principles approach is advantageous for global change research because the combination of life-history traits of competitors interact to cause a site-specific dynamic response to fundamental drivers (e.g., precipitation, temperature), and these site-level responses interact spatially to create landscape responses that are complex and difficult to project with less mechanistic approaches, and (2) published findings that increasing drought length (rather than severity) increases tree mortality in the upper Midwest are clearly consistent with a mechanism of acute photosynthetic depression resulting in increased likelihood of carbon starvation as droughts lengthen.

Key words: climate change; drought-induced mortality; first principles; forest succession; LANDIS-II; mechanistic landscape model; PnET-Succession; water stress.

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INTRODUCTION

Climate change is expected to increase the frequency and intensity of drought events in much of the world (IPCC 2013). This will impact forest dynamics and composition through direct (altered growth, competition, and mortality) and indirect (altered disturbance regimes) effects. Forest managers must account for both direct and indirect effects of climate change on forest landscape dynamics, including the potentially large impact of increasing drought conditions. However, forested ecosystems are structured by a number of complex and interacting processes (e.g., seed dispersal, establishment, growth, competition, disturbance), most of which have the potential to be modified by a changing climate, making predictions intimidating and fraught with uncertainty (Dale et al. 2001).

For managers of large land areas, forest landscape models (FLMs) have proved useful for projecting future forest dynamics because they account for most of the factors that structure forested ecosystems at landscape spatial and temporal scales (He 2008). FLMs simulate these dynamics at a spatial scale intermediate between stand models (e.g., Forest-GCB, Running and Gower 1991, PnET-CN, Aber et al. 1997) that simulate growth and materials fluxes within a forest stand and dynamic global vegetation models (DGVM, e.g., SEIB–DGVM; Sato et al. 2007) that simulate competition among vegetation types (e.g., biomes) at regional to global scales (Medlyn et al. 2011). Unlike stand and DGVM models, FLMs are spatially explicit, simulate competition and succession at the species level, and simulate dispersal and disturbance as distinct processes such that their interactions play out as an emergent property of the climate inputs. However, because of these added processes, they generally simplify the simulation of growth and competition compared to stand and DGVM models and are constructed using a mixture of mechanistic and phenomenological components. Mechanistic components explicitly model cause and effect mechanisms that result in growth, mortality, and succession on forested sites (De Bruijn et al. 2011), incurring greater computational costs and parameterization burden and uncertainty. Phenomenological (sometimes called empirical or statistical) components model system out-

comes using surrogate computational functions that mimic the effects of the mechanism, often based on how the system has behaved in the past (Schelhaas et al. 2004), resulting in uncertainty when extrapolating the phenomenological relationships beyond the domain in which they were developed to the novel conditions of the future (Keane et al. 2015). Both approaches result in considerable uncertainty, but the extrapolation uncertainty of the phenomenological approach has increasingly been deemed to exceed the parameter uncertainty of the mechanistic approach (Cuddington et al. 2013, Gustafson 2013).

Most FLMs do not incorporate drought effects on tree growth except as an environmental filter affecting establishment, with a few exceptions. The tree-based FLM iLand (Seidl et al. 2012) includes ecophysiology processes that conceptually include drought as a stressor, but such behavior has not yet been explored. In FireBGCv2 (Keane et al. 2011), photosynthetic growth reductions caused by soil water stress can optionally be modeled. Gustafson and Sturtevant (2013) developed a phenomenological drought disturbance extension for LANDIS-II, but it may lack necessary robustness under future conditions. Often drought weakens trees and makes them more vulnerable to other disturbances, which are included in FLMs. However, because the links between drought, physiological stress and disturbance are rudimentary in FLMs, the ability of most FLMs to reliably project the cumulative effects of increased incidence of drought is weak. Furthermore, drought effects are likely to propagate through many of the process interactions that ultimately determine successional outcomes in forested ecosystems, and such ability is currently beyond the capability of most FLMs. For example, drought increases water stress and reduces photosynthesis, which can be exacerbated by elevated temperatures that increase evapotranspiration (Williams et al. 2013), although elevated CO_2 can mitigate growth reductions when water stress reduces stomatal conductance (Franks et al. 2013). Cloudiness may also decrease with drought, which increases photosynthetically active radiation (PAR) and therefore photosynthetic activity and transpiration. However, species vary in their ability to compete for water, tolerate water stress, and their optimal temperature for photosynthesis, which should

result in altered successional outcomes under the conditions of the future. Species also vary in the disturbances to which they become susceptible when they are physiologically stressed, and disturbance regimes themselves may be significantly altered as climate changes (e.g., temperature-dependent insect pests, fire). Furthermore, the robustness of drought-related impacts on disturbance regimes is highly variable within FLMs, in some cases further weakening the links between drought and landscape forest dynamics.

Gustafson and Sturtevant's (2013) phenomenological approach to model tree mortality caused by drought within the LANDIS-II FLM used empirical relationships found between the length of drought events (defined as consecutive years with mean Palmer Drought Severity Index < −0.5) and species biomass lost to mortality on long-term Forest Service Forest Inventory and Analysis (FIA) plots during the period of record (1977–2009) in the upper Midwest. To model these empirical findings, drought events are drawn from a statistical distribution of drought length supplied by the user and biomass is removed from tree species cohorts (oldest first) according to such empirical relationships. Although the approach shows promise, it is not without difficulties. Estimating the empirical relationships requires inventory data over a long time period that encompasses both droughts and wet periods, and the drought signal in those data is noisy because it includes all mortality, some of which may not be drought-induced. Therefore, many observations are required. Furthermore, the generality of those relationships has yet to be demonstrated. Gustafson (2014) attempted to apply the relationships estimated by Gustafson and Sturtevant (2013) to a similar ecological Province in the northeastern United States with limited success. The approach also does not account for the differential effects of drought on species growth and competition, and although the simulated mortality may account for mortality caused by disturbance (e.g., insects), there are no explicit links between drought stress and specific disturbances.

A more mechanistic approach to simulate forest growth and succession in an FLM was recently developed by De Bruijn et al. (2014) by embedding algorithms of the PnET-II stand-level ecophysiology model (Aber et al. 1995) in a LANDIS-II succession extension (PnET-Succession) to mechanistically simulate biomass growth as a competition for light and water to support photosynthesis. Generally, LANDIS-II succession extensions simulate growth and competition among tree species cohorts using life-history attributes such as maximum aboveground net primary productivity, shade tolerance, longevity, and seed vagility. The PnET-Succession extension also includes physiological attributes such as light saturation intensity, water use efficiency and drought tolerance that allow the realized niche of species to emerge through time (*sensu* Huston and Smith 1987). PnET-Succession models soil water monthly as a function of soil texture, precipitation, interception, evaporation, and consumption by trees (similar to DGVMs), allowing response to extreme drought events rather than being limited to the mean weather values (typically decadal) used by less mechanistic approaches. Accordingly, photosynthetic rates (and therefore growth rates) vary monthly by species and cohorts as a function of precipitation and temperature (among other factors), which directly affect competition and ultimately successional outcomes.

The opportunities afforded by this approach for simulating drought effects on forests are significant. First, because there are several parameters related to drought tolerance (including cohort establishment), the differential effects of drought on the ability of species to compete can result in altered successional outcomes through time. These outcomes are an emergent property of the mechanistic simulation of growth that accounts for the interaction of precipitation, temperature, light (including seasonal cloudiness), CO_2 concentration, and species' physiological attributes, rather than phenomenological estimates of their combined effects based on behavior seen in the past. Second, because the extension tracks carbon reserves, drought-induced growth reductions can cause carbon reserves to become depleted by respiration, which can result in direct mortality (McDowell et al. 2013), or the level of carbon reserves can be used by disturbance extensions to realistically target disturbance-induced mortality to stressed cohorts (complete or partial mortality of cohorts). Physiological stress may be dependent on either the intensity or duration of water limitations (or both) depend-

ing on the ability of a species to extract water from the soil and maintenance respiration rates, including interactions with all the other factors that affect growth (e.g., light, temperature, CO_2). For studies of the effects of climate change on forest successional dynamics, a weather stream of temperature, precipitation and radiation from downscaled global circulation models can allow growth and establishment rates to vary monthly, rather than using longer term averages that make it difficult to simulate extreme events. Drought-induced mortality is simulated when moisture stress depresses growth rates below respiration levels long enough to reduce carbon reserves below survival thresholds, or when a disturbance targets stressed cohorts.

The more mechanistic approach to modeling drought effects at landscape scales is conceptually appealing because of its reliance on first principles and ecological theory, but it is difficult to test, primarily because appropriate data sets are rare and because drought can rarely be definitively identified as the ultimate cause of mortality. Gustafson et al. (2015) used PnET-Succession to predict the outcome of a precipitation manipulation experiment in a piñon-juniper ecosystem in New Mexico (USA), with considerable success. Importantly, they discovered that the amount of nonstructural carbon reserves (NSC) predicted by PnET-Succession was negatively related to the incidence of mortality on experimental plots. Although this model test was promising, the authors indicated that tests using other species are needed. The tree species in the upper Midwest (USA) studied by Gustafson and Sturtevant (2013) provide an opportunity to study whether the physiological behavior simulated by PnET-Succession is consistent with their empirical relationships between drought and plot-level tree mortality.

The objectives for this study were to (1) explore how physiological mechanisms explain the empirical results of Gustafson and Sturtevant (2013) by using PnET-Succession to conduct controlled site-level simulation experiments that vary the driving variable (length of drought) found in that study, (2) confirm the applicability of PnET-Succession for simulating drought effects in mixed temperate forests, (3) determine how species competition, landscape pattern (i.e., soils), and spatial processes (i.e., seed disper-

sal and stand-replacing disturbance) interact to determine forest composition dynamics under drought conditions by conducting a landscape-level drought simulation experiment, and (4) assess the potential advantages and disadvantages of the mechanistic approach for simulating drought effects in FLMs.

MATERIALS AND METHODS

Simulation model

LANDIS-II (Scheller et al. 2007) simulates broad-scale ($>10^5$ ha) forested landscape dynamics over long (i.e., centuries) temporal scales, including succession, multiple natural disturbance types, seed dispersal, forest management, and climate change effects. Landscapes are represented as a grid of interacting cells with user-defined cell size. Individual cells are assumed to have homogeneous canopy layering, and are spatially aggregated into land types with homogeneous climate and soils. Forest composition at the cell level is represented as age cohorts of individual tree species that interact via a suite of vital attributes (e.g., growth capacity, shade tolerance, drought tolerance, seed dispersal, longevity) to produce nondeterministic successional pathways sensitive to disturbance type and severity (Mladenoff 2004).

PnET-Succession (De Bruijn et al. 2014) is one of several available LANDIS-II succession extensions, and it projects tree cohort growth by mechanistically simulating photosynthetic output. In PnET-Succession, soil water is tracked at the grid-cell level using a bulk-hydrology model based on precipitation, loss to foliage interception, evaporation, runoff and percolation out of the rooting zone, and consumption by species cohorts. Tree cohorts compete for water and light in each cell. Cohort biomass (an indicator of relative tree size) determines the priority of access to light, while access to soil moisture is evenly distributed among cohorts. When water is adequate, the rate of photosynthesis for a given species cohort increases with light available to the cohort (dependent on canopy position and leaf area), atmospheric CO_2 concentration and foliar N, and decreases with age and departure from optimal temperature. As soil water availability decreases, photosynthesis also decreases. PnET-Succession accounts for reductions in

Table 1. Water availability characteristics of the soil types used in the experiments.

Soil type	Abbreviation	Rooting depth (m)	Field capacity (mm)†	Wilting point (mm)‡	PAW (mm)§
Sand	SAND	1.0	100.5	40.2	60.3
Sandy loam	SALO	1.0	188.6	81.4	107.2
Loam	LOAM	1.0	285.9	135.6	150.3
Silt loam	SILO	1.0	341.1	129.3	211.8

† At −0.033 MPa soil water potential.
‡ At −1.5 MPa soil water potential. Actual wilting point for each species varies depending on parameterization of H4 (see Table 2).
§ PAW = Plant Available Water (Soil field capacity minus wilting point). Actual PAW for each species varies depending on the species drought tolerance and their H3/H4 parameterizations (Table 2).

photosynthesis due to foliar and maintenance respiration using a Q10 relationship, where a 10 °C increase in temperature results in a 10-fold increase in respiration rate (Atkins 1978), such that foliar respiration rate depends on temperature and moisture, while maintenance respiration depends on temperature and biomass. Thus, growth rates vary monthly by species and cohorts as a function of precipitation, temperature and species traits, which directly affects competition and ultimately successional outcomes. Capitalizing on this approach, drought-induced growth reductions result from water stress, and mortality can result if carbon reserves become depleted by respiration. Such mortality may be dependent on both the intensity and duration of water limitations, depending on the ability of a species to extract water from the soil and tissue maintenance costs. A weather stream of monthly temperature, precipitation and radiation allows growth and establishment rates to vary dynamically, and drought-induced mortality is simulated when moisture stress depresses growth rates below respiration levels long enough to reduce carbon reserves below survival thresholds.

In our study, we used PnET-Succession v1.2. The major change from v1.0 (De Bruijn et al. 2014) is a modification of the algorithms to simulate soil water (Gustafson and De Bruijn 2015). Rather than a simple bucket hydrology approach, v1.2 calculates plant available water (PAW) based on soil texture and precipitation inputs and losses. Moisture stress is related to soil water potential, which varies predictably depending on soil water content and the soil type (Feddes et al. 1978). Saxton and Rawls (2006) provide equations to estimate water retention curves for soils based on soil texture characteristics commonly avail-

Table 2. PnET-Succession drought tolerance water potential parameters used for the experimental levels of the drought tolerance factor, arbitrarily assigned based on Fig. 5 in Limousin et al. (2013).

Tolerance class	H3 (MPa)	H4 (MPa)
Drought-intolerant	−0.98	−1.47
Somewhat drought-intolerant	−1.12	−2.30
Somewhat drought-tolerant	−1.28	−3.72
Drought-tolerant	−1.47	−5.88

able from soil surveys (% sand, % silt, % clay, % organic matter, % gravel, salinity), and we used their average soil attributes for each soil type. The input loss parameters and PAW characteristics for our soil types are given in Appendix S1 and Table 1. Water stress in PnET-Succession for a species cohort is calculated from soil water potential using four species-specific water potential thresholds (H1-H4, Feddes et al. 1978). H1 and H2 control the effects of waterlogging on photosynthesis and default values (0.0) were used for this study, which means that photosynthesis reductions due to excess of water did not occur. H3 specifies the soil water potential at which reductions in photosynthesis begin to occur and H4 specifies the potential at which photosynthesis ceases (Table 2), which has the effect of determining how much of the soil water is actually available to the species.

Model calibration

Although the PnET-Succession extension of LANDIS-II primarily uses parameters that can be estimated from the literature, modest calibration of some parameters is required. Prior to simulations the growth rate of each species

was calibrated by simulating a monoculture of each species for 140 yr on the soil type where it is typically found, using the average climate. First, established parameter values (e.g., foliar nitrogen (FolN), maximum specific leaf weight (SLWmax), half-saturation light level (HalfSat)) were set in the center of the range of published values (Appendices S1 and S2). Because potential photosynthetic capacity (Amax) is proportional to FolN in PnET-Succession, FolN was adjusted within empirical limits to reflect relative growth rate observed among species as documented in a silviculture manual (Burns and Honkala 1990). Maintenance respiration rate has a profound effect on drought mortality, and was held constant among species to avoid confounding the drought tolerance treatment. PnET-Succession assumes that the amount of foliage biomass of a cohort is determined by the amount of xylem tissue available to transport water, which is assumed to be proportional to woody biomass. The FracFol variable (Appendix S2) specifies this proportion and FracActWd controls an exponential decline function that reflects the loss of active xylem tissue to heartwood as cohorts increase in size. The amount of foliage determines carbon fixation and biomass production given photosynthetic capacity, so FracFol was calibrated to control how quickly biomass reaches an arbitrary milestone (5 kg/m^2), with the empirically fastest growing species reaching the milestone in 27 yr and the slowest in 31. The maximum biomass attained was controlled using the water use efficiency constant (WUEc). Leaf area index was controlled using SLWmax and FracActWd, and was calibrated to fall within the range of empirical values for each species as found throughout the literature. Simulated growth was calibrated to match growth (aboveground biomass) found in growth and yield tables (e.g., Burns and Honkala (1990) and other published sources (listed in Supplement S1). When biomass was estimated from volume data, dry wood specific gravity from Miles and Smith (2009) was used. Species for which no growth tables were found (balsam poplar, bitternut hickory, pin oak, bur oak, red maple, black cherry, yellow birch, beech) were calibrated to mimic the growth of species with similar life-history and growth traits. Belowground fraction was estimated by

comparing aboveground biomass estimates to total above and below ground biomass estimates of Smith et al. (2006). In general, we held as many parameters constant as possible to increase confidence that the behavior of the response variables was caused by the experimental treatments. If more parameters varied among species then there would be greater uncertainty about which parameters were driving the results. Plots of calibrated biomass growth curves overlaid on empirical measurements are available in Supplement S1.

Site-level experiment

A site-level (single cell) experiment was conducted using a full-factorial design with three factors: (1) species drought tolerance (four levels), (2) soil texture (four levels), and (3) length of drought (three levels). Species drought tolerance was considered a fixed treatment effect, and we used the four *a priori* drought tolerance classes of Gustafson and Sturtevant (2013), modified slightly by Pastor and Post (1986) (Table 3). We assigned PnET-Succession parameter values to reflect the response of each drought tolerance class to water stress, generically defining these values based on relationships between photosynthesis and water potential (Limousin et al. 2013, Table 2). We simulated four distinct species assemblages because species have other life-history traits that vary independently from drought tolerance and may interact with drought tolerance in complex ways. One species (cohort age = 80 yr) from each drought tolerance class was arbitrarily assigned to each of these assemblages, with each assemblage containing species that might be found on similar sites (Table 4).

Soil texture was included as a block factor because soil texture may have a large effect on the availability of water for tree photosynthesis given precipitation inputs. We set the levels of the soil factor across a gradient of increasing plant available water (PAW), defined as field capacity (water content at −0.033 MPa of water potential) minus wilting point (water content at −1.5 MPa of water potential), using four standard soil texture classes (sand, sandy loam, loam, silt loam) (Saxton and Rawls 2004) (Table 1). Length of drought events was included as a fixed treatment effect because Gustafson and Sturtevant (2013) found

Table 3. Species simulated and their assignment to the four drought sensitivity classes, based on Gustafson and Sturtevant (2013) and Pastor and Post (1986).

Drought sensitivity class	Common name	Scientific name	Abbreviation
Intolerant	Balsam poplar, Quaking aspen, big-toothed aspen, paper birch, black ash	*Populus balsamifera, P. tremuloides, P. grandidentata, Betula papyrifera, Fraxinus nigra*	popubal, poputre, popugra, betupap, fraxnig
Somewhat intolerant	Eastern hemlock, sugar maple, northern white cedar, yellow birch, balsam fir, bitternut hickory	*Tsuga canadensis, Acer saccharum, Thuja occidentalis, Betula alleghaniensis, Abies balsamea, Carya cordiformes*	tsugcan, acersac, thujacc, betuall, abiebal, carycor
Somewhat tolerant	Red maple, black cherry, white ash, green ash, basswood, red oak, American larch, white spruce, black spruce, American beech	*Acer rubrum, Prunus serotinus, Fraxinus americana, F. pennsylvanica, Quercus rubra, Tilia americana, Picea glauca, P. mariana, Fagus grandifolia*	acerrub, prunser, fraxame, fraxpen, querrub, tiliame, picegla, picemar, fagugra
Tolerant	Red pine, white pine, jack pine, white oak, northern pin oak, bur oak	*Pinus resinosa, P. strobus, P. banksiana, Quercus alba, Q. ellipsoidalis, Q. macrocarpa*	pinures, pinustro, pinuban, queralb, querell, quermac

Table 4. Species composition of the experimental assemblages.

Drought tolerance class	Assemblage 1	Assemblage 2	Assemblage 3	Assemblage 4
Drought-intolerant	*Populus grandidentata*	*Populus tremuloides*	*Betula papyrifera*	*Fraxinus nigra*
Somewhat drought-intolerant	*Acer saccharum*	*Abies balsamea*	*Tsuga canadensis*	*Thuja occidentalis*
Somewhat drought-tolerant	*Fraxinus americana*	*Picea glauca*	*Quercus rubra*	*Acer rubrum*
Drought-tolerant	*Quercus alba*	*Pinus banksiana*	*Pinus resinosa*	*Pinus strobus*

that drought-induced tree mortality was most related to drought length in the upper Midwest. We set three levels of length of drought events (2, 4, 8 yr) to fall within the range empirically analyzed by Gustafson and Sturtevant (2013). We used a highly simplified weather stream to produce a clear drought signal. Based on weather data from Oconto county (Wisconsin, USA) we used fixed monthly averages of temperature, precipitation and PAR for the spin-up period (80 yr) and nondrought years, and reduced those precipitation values by 90% in growing season months (May–September) and by 75% in nongrowing season months in drought years to create a strong drought signal. During the spin-up period, PnET-Succession simulates initial cohorts from establishment to their condition at the start of the experiment. Temperature and PAR did not vary by treatment and CO_2 was held constant at 400 ppm.

All simulations were run on a single 30-m cell to mimic the FIA plots used by Gustafson and Sturtevant (2013), where species compete for water and light, and response to drought is at least partially a function of inter-specific competition. In each assemblage, a single cohort of each of the four species was established on an empty cell in 1930 and grown for 80 yr using a constant, average climate (spin-up). Longevity of all species was set to 200 yr to avoid the confounding effect of senescence. The drought treatments were applied beginning in 2010, and were comprised of alternating periods of normal precipitation and drought events for 36 yr, with the total number of years of drought held constant across treatments. The 2-yr drought length treatment alternated 1 yr of normal precipitation and 2-yr droughts, the 4-yr drought length treatment alternated 2 yr of normal precipitation and 4-yr droughts and

the 8-yr drought length treatment alternated 4 yr of normal precipitation and 8-yr droughts. All treatments resulted in 12 yr of normal precipitation and 24 yr of drought. Three replicates of each factorial combination were produced.

Analysis

Because the response of species to the dynamic treatments was also dynamic, the simulation results were evaluated by plotting mean values of response variables through time and visually comparing the variation in response variables across treatments and factors. Our objective was not to quantify the significance of differences at an instant of simulated time, but to assess how the model predicted the dynamics of plant response to droughts under different abiotic and competitive environments. Our expectation was that the relative magnitude of reductions in photosynthesis and NSC would be directly related to the drought tolerance parameters (H3, H4), and that longer droughts would result in greater reductions. The temporal characteristics of response to drought events (i.e., lag, rate of reduction and recovery) were an important part of the study. We also sought to gain insight into how life-history traits may interact with drought sensitivity through the competitive interactions within the various assemblages. Net photosynthesis was evaluated because it is the keystone growth and competition variable that is directly related to water stress (Chaves et al. 2002). NSC fraction was evaluated because it represents carbon reserves, which are believed to be an indicator of plant stress and inversely correlated with likelihood of mortality (McDowell et al. 2013, Gustafson et al. 2015). Woody biomass was evaluated because change in biomass reflects photosynthetic output and competition, and was the variable evaluated by Gustafson and Sturtevant (2013).

Landscape-level experiment

We conducted a landscape-level experiment to evaluate how species competition, landscape pattern (i.e., soils) and spatial processes (i.e., seed dispersal and stand-replacing disturbance) may interact to determine forest composition dynamics under drought conditions. The experiment was conducted on a 104 471 ha

landscape in Oconto County (Wisconsin, USA) that has a variety of soil types (Fig. 1). This experiment included the site experiment factors of drought tolerance classes, soil and drought, but the drought treatment was implemented differently to create a simulation long enough to allow a successional response to the treatments. The drought factor had two levels: control (historical weather stream) and drought (periodic 8-yr droughts as in the site experiment). The weather stream was derived from spatially interpolated gridded weather data for our study area (Fig. 1) obtained from the USGS Geodata Portal, representing averaged daily records from 1949 to 2010 (Maurer et al. 2002). Because the historical weather stream extended only between 1949 and 2010, we used long-term monthly averages (1949–2010) for the spin-up period (oldest initial cohort = 210 yr) and appended copies of the historical stream to represent future years to create a weather stream extending to 2190. All other variables were unchanged from the site experiment. We did not include temperature or CO_2 concentration change to avoid confounding interpretation of results relative to the site experiment. Variation in soil type was included in the ecoregion map (Fig. 1). Topographic relief is minimal and climate is essentially homogeneous across the study area. The ecoregion map was produced by assigning all SSURGO (Soil Survey Staff 2013) soil map polygons to the most similar of the four soil types used in the site experiment. The initial forest conditions (species and age cohorts) were those used by Janowiak et al. (2014), created using the methods of Wilson et al. (2012).

Tree species establishment probability is calculated dynamically by the model and is inversely proportional to light and water stress for each species on each site at each time step. In the absence of disturbance we would expect the establishment of more shade-intolerant species to decline on the landscape for reasons unrelated to drought. We therefore simulated a generic, stand-replacing disturbance regime using the Base Harvest disturbance extension (Gustafson et al. 2000). We arbitrarily defined a grid of 5.8 ha (8 × 8 cells) stands across the landscape grid, and simulated complete removal of all cohorts of all species within a randomly selected 3.3% of the stands each decade (300 yr return interval). This
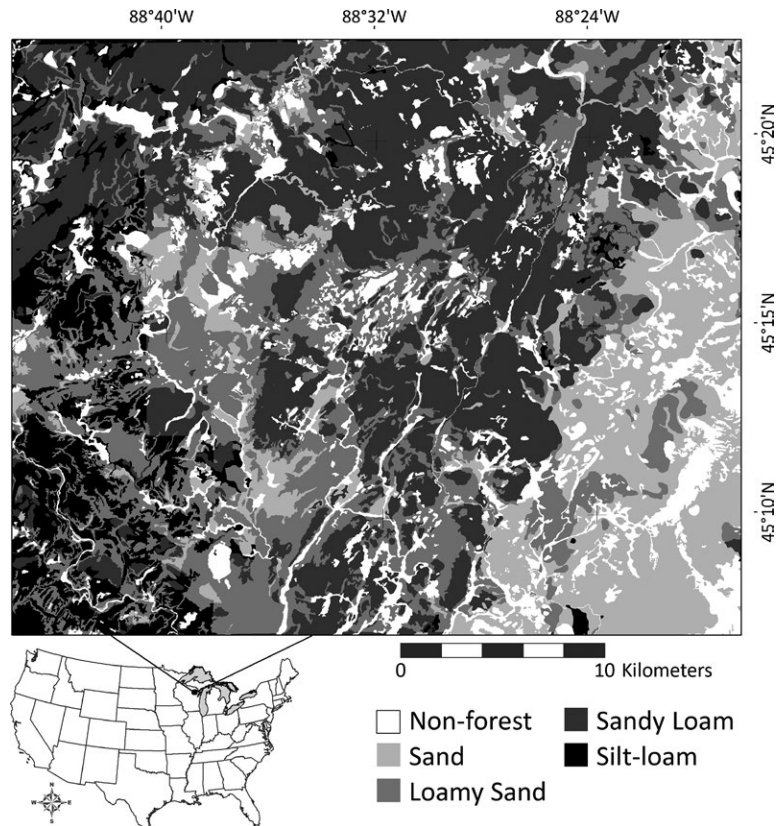
Fig. 1.   Ecoregions (soil types) used in the study area in Oconto county (WI), mapped at 30 m resolution.

disturbance regime was not intended to mimic any real disturbance agent(s), but to introduce controlled disturbances to meet the experimental objectives. Stands were not selected for disturbance unless the youngest cohort age was at least 21 yr. All extensions used a 10-yr time step and three replicates of each drought scenario were simulated for 180 yr.

RESULTS

Site experiment

The reduction in carbon reserves (NSCfrac) was quicker and more pronounced as length of droughts increased on all soil types (Fig. 2). Relative species' drought tolerance (higher H3 and H4) also lessened the reduction in NSCfrac associated with increasing drought length, with the most drought tolerant species almost completely unaffected by droughts of any length. This phenomenon was ultimately driven by net photosynthesis (NetPsn), which showed a clear

response to both the length of drought and the alternating pulses of normal precipitation and drought events on all soils (Fig. 3).

Increasing PAW (SAND to SILO) also lessened the reduction in NSCfrac associated with droughts of all lengths, although the difference between LOAM and SILO was modest (Fig. 2). The longer persistence of the somewhat drought-intolerant acersac (sugar maple) on the SAND compared to SALO soil type is likely a consequence of lower maintenance respiration costs of the lesser acersac biomass on the SAND soil (Fig. 4). Similarly, the lack of much difference between LOAM and SILO NSCfrac curves (Fig. 2) may be the result of higher biomass and consequently higher maintenance respiration costs on the SILO soil. The amount of biomass prior to the treatments (beginning in 2010) increased as PAW increased for the two relatively drought-intolerant species and decreased for the relatively drought-tolerant species (Fig. 4), presumably because of the relative importance of competition
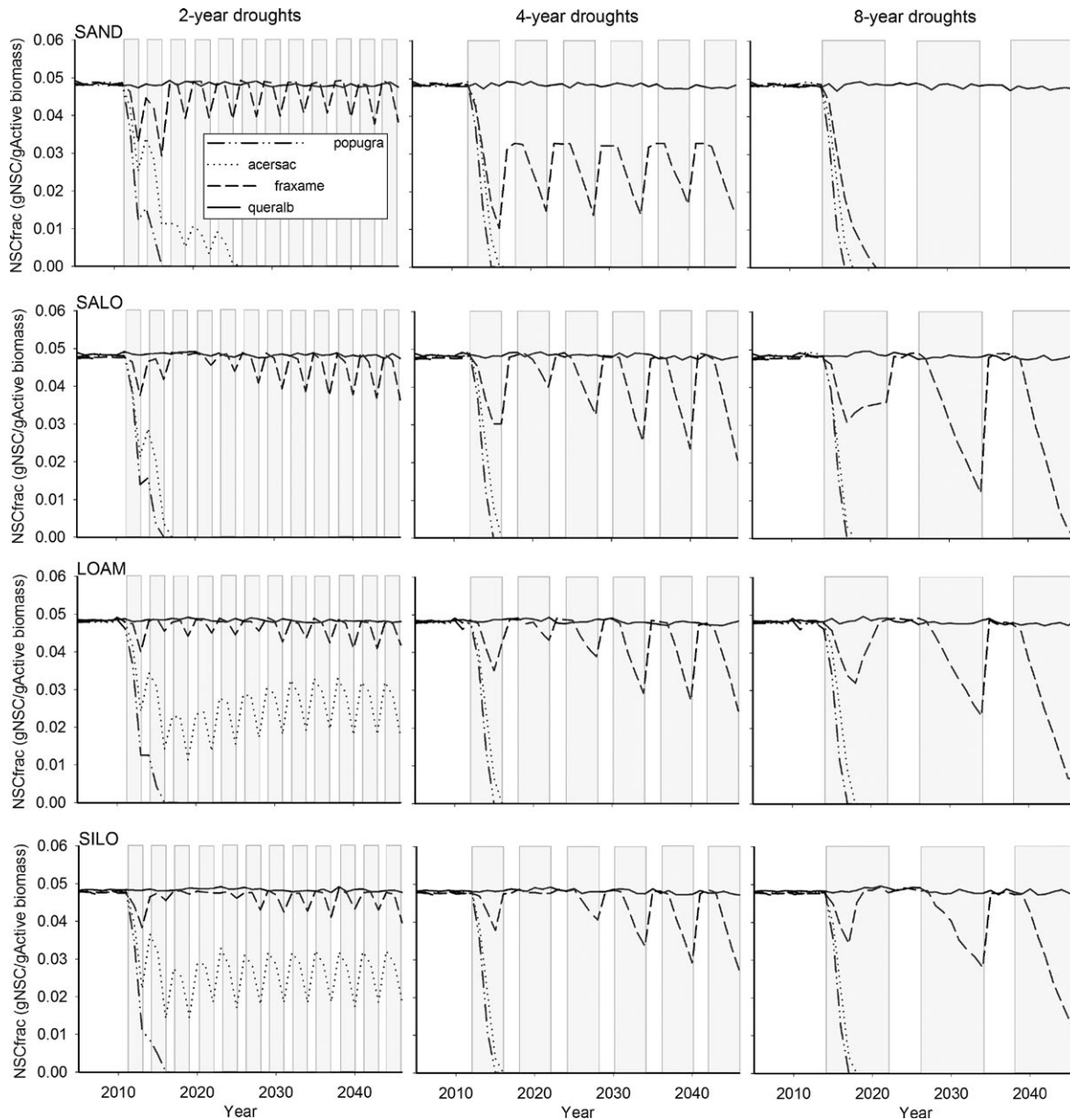
Fig. 2. Comparison of the response of carbon reserves (NSCfrac) of Assemblage 1 species to the length of drought and soil type experimental factors. Plant available water increases evenly from sand to silt loam (Table 1). Gray boxes indicate periods of drought. Cohorts died when NSCfrac <0.01 at the end of a simulation year. The mean of three replicates is shown; replicate variability is not shown for clarity.

for light vs. water on the various soils. The rate of biomass growth during drought treatments was marginally higher with increasing PAW. The height of the precipitation-induced peaks and valleys of NetPsn for relatively drought-tolerant species was determined more by the number of competitors than by PAW, while for relatively

drought-intolerant species, it was determined by PAW (Fig. 3). Total site NetPsn increased with increasing PAW during normal precipitation periods, but not during droughts (not explicitly shown). Biomass of drought tolerant species increased during droughts as less drought tolerant competitors died.
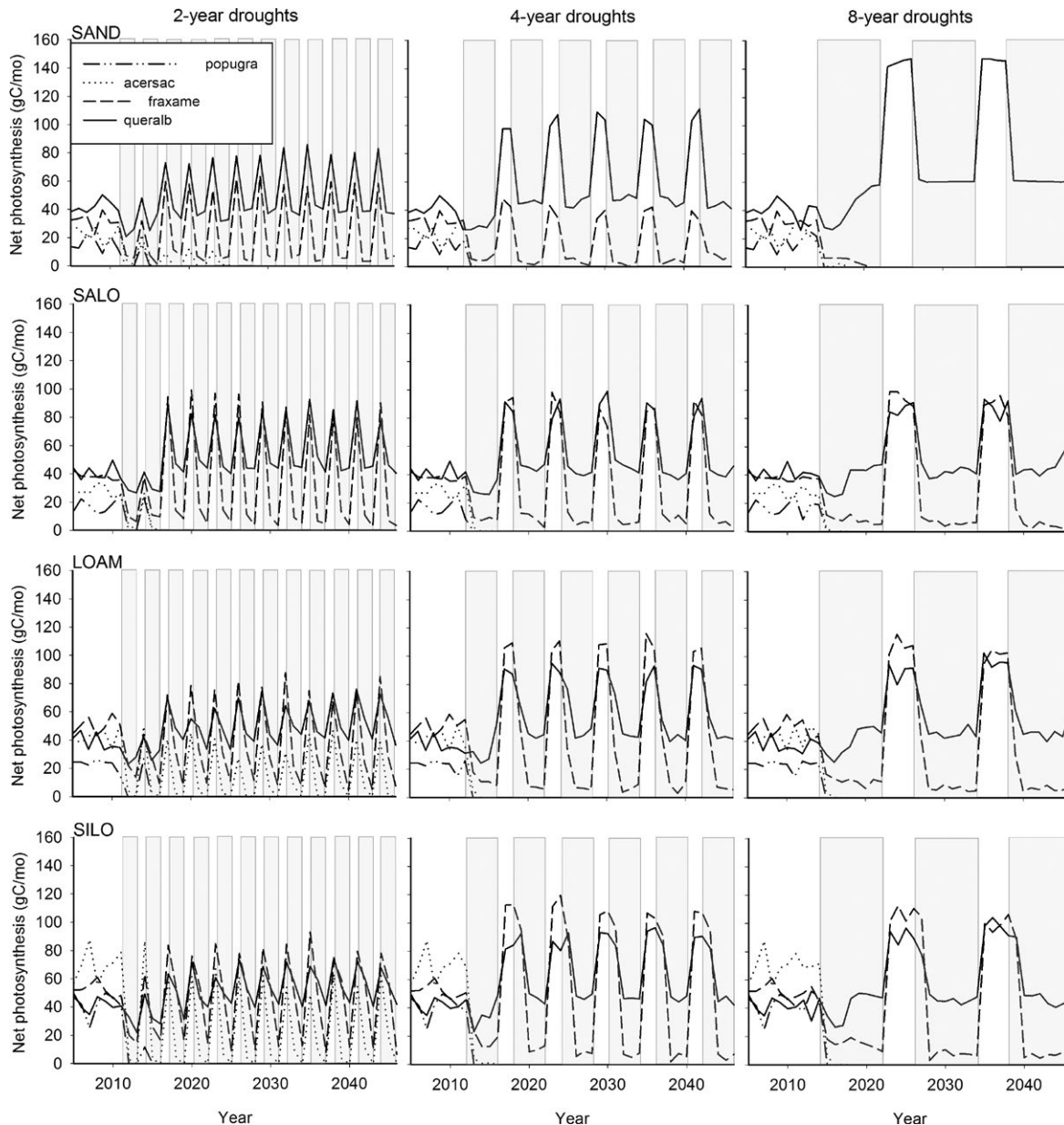
Fig. 3. Comparison of the response of net photosynthesis of Assemblage 1 species to the length of drought and soil type experimental factors. Plant available water increases evenly from sand to silt loam (Table 1). Gray boxes indicate periods of drought. Cohorts died when NSCfrac <0.01 at the end of a simulation year. The mean of three replicates is shown; replicate variability is not shown for clarity.

The effect of the drought treatments varied depending on the assemblage of competitors with varying life-history traits such as ability to compete for light (HalfSat), maximum photosynthetic capacity (FolN, SLWmax, Amax), and water use efficiency. For example, the slower growing, somewhat drought-intolerant species in Assemblage 1 (acersac) displays NSCfrac dynamics very similar to that of the drought-intolerant species (popugra) under all drought treatments (Fig. 5), while the faster growing analogous species in Assemblage 2 (abiebal, see Fig. 6)
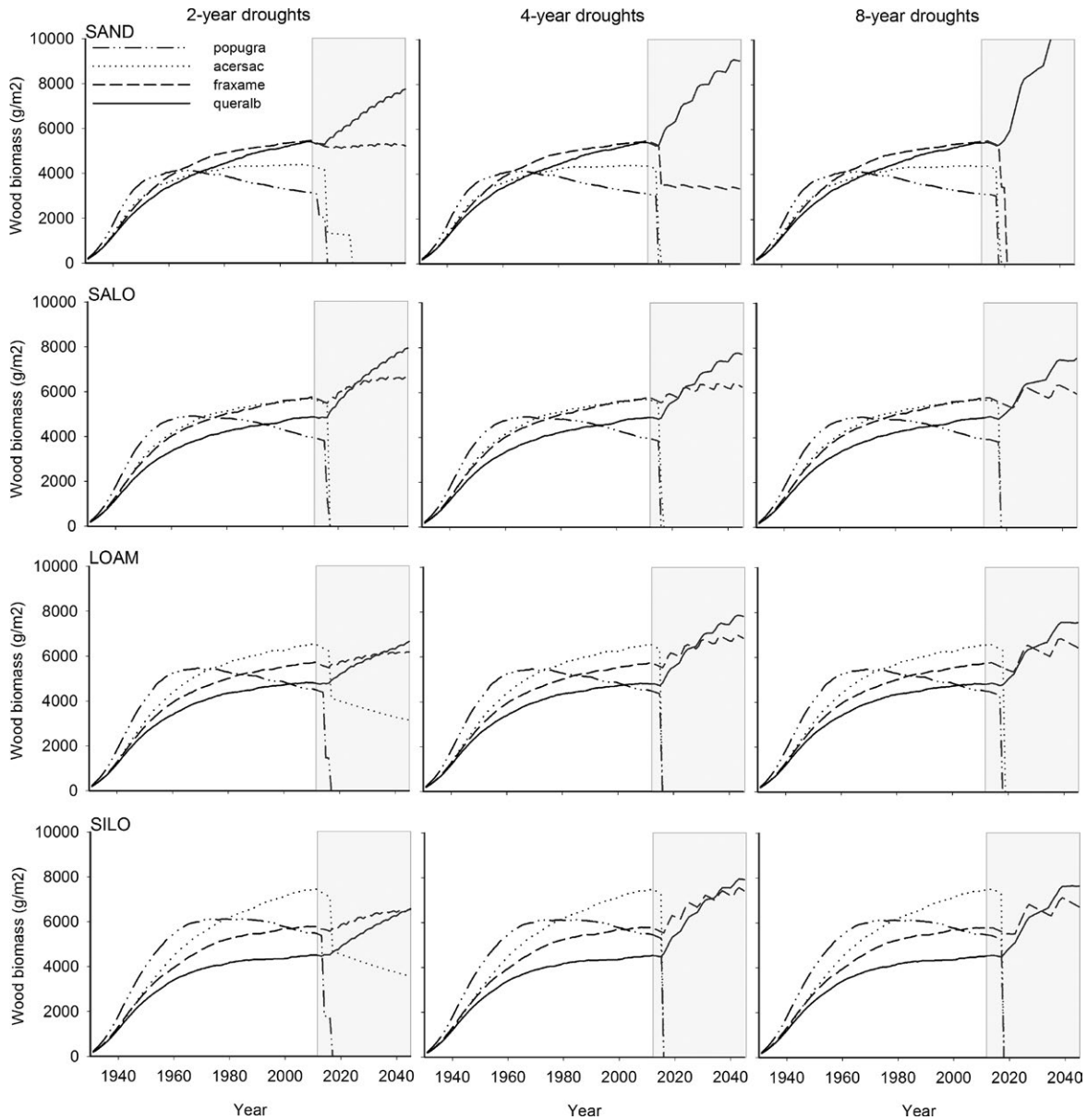
Fig. 4. Aboveground woody biomass through simulated time of Assemblage 1 species to the length of drought and soil type experimental factors. Plant available water increases evenly from sand to silt loam (Table 1). Gray boxes indicate the period when drought treatments were applied. Cohorts died when NSCfrac <0.01 at the end of a simulation year. The mean of three replicates is shown; replicate variability is not shown for clarity.

persists under all drought treatments. In some cases, both of the relatively drought-tolerant species show little response to even the longest droughts (Assemblages 2 and 3), whereas in Assemblage 1, the somewhat drought-tolerant species eventually succumbs to 8-yr droughts. Generally, as competing cohorts die, the remain-ing cohorts are better able to maintain NSCfrac levels during subsequent droughts. However, in the presence of a rapidly growing competi-tor with more drought tolerance, this effect may be short-lived, as seen by fraxame in Assem-blage 1 and acerrub in Assemblage 4 (Fig. 5). This happens because the increasingly large
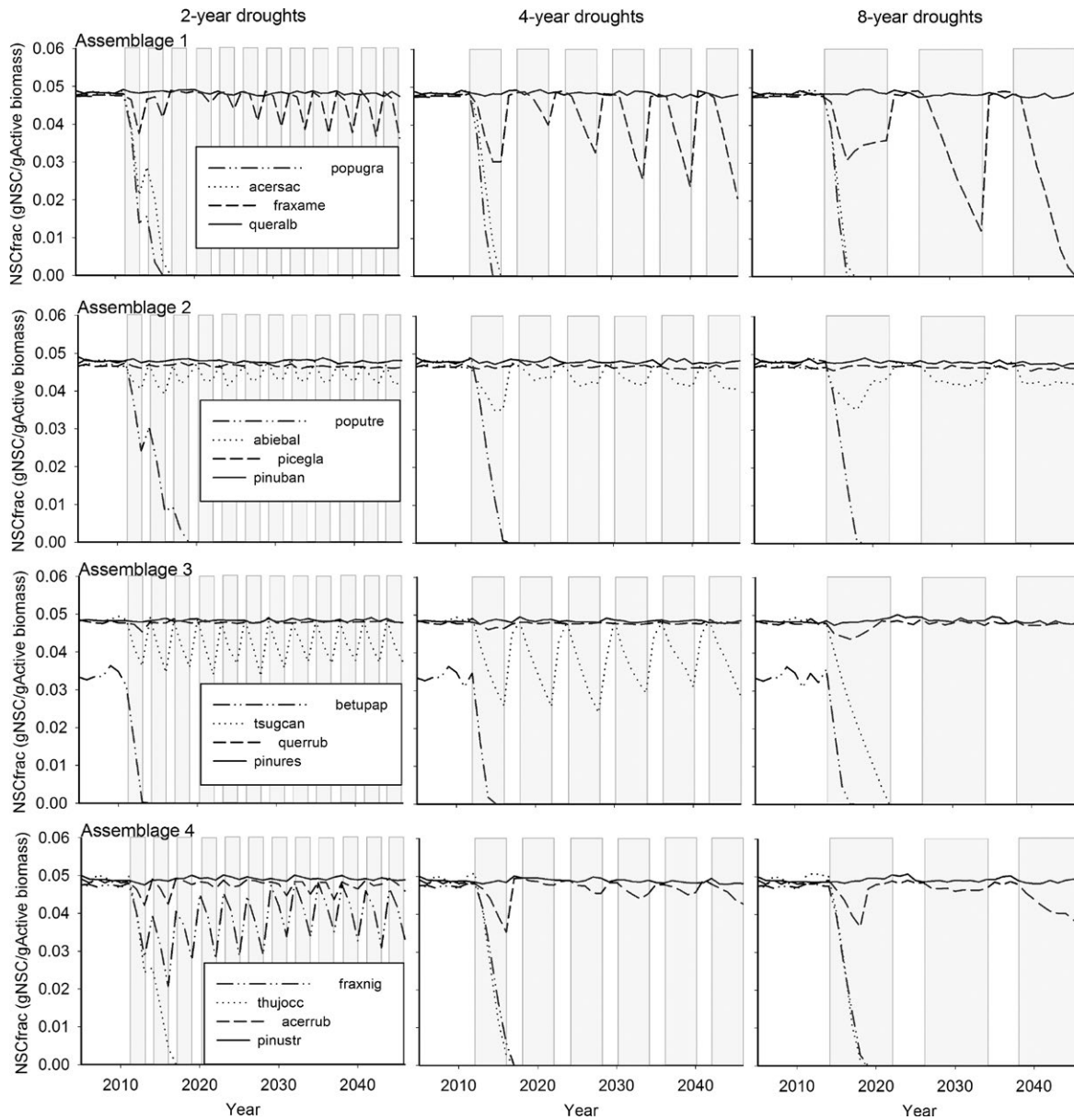
Fig. 5. Comparison of the response of carbon reserves (NSCfrac) of Assemblages to the length of drought and soil type experimental factors on a sandy loam soil. Gray boxes indicate periods of drought. Cohorts died when NSCfrac <0.01 at the end of a simulation year. The mean of three replicates is shown; replicate variability is not shown for clarity.

cohorts consume water more quickly, reducing site water potential below the H4 value of the less drought-tolerant species more quickly. Assemblage 4 is unique because the fast-growing, most drought-intolerant species (fraxnig), is not the first to succumb to drought. NetPsn of northern white cedar (thujocc) drops to nearly zero during droughts and its very low photosynthetic capacity is unable to restore carbon reserves between droughts of even just 2 yr (given these competitors (Fig. 7)), dramatically illustrating the potential interaction between H3/H4 (drought tolerance) and Amax (photosynthetic capacity).
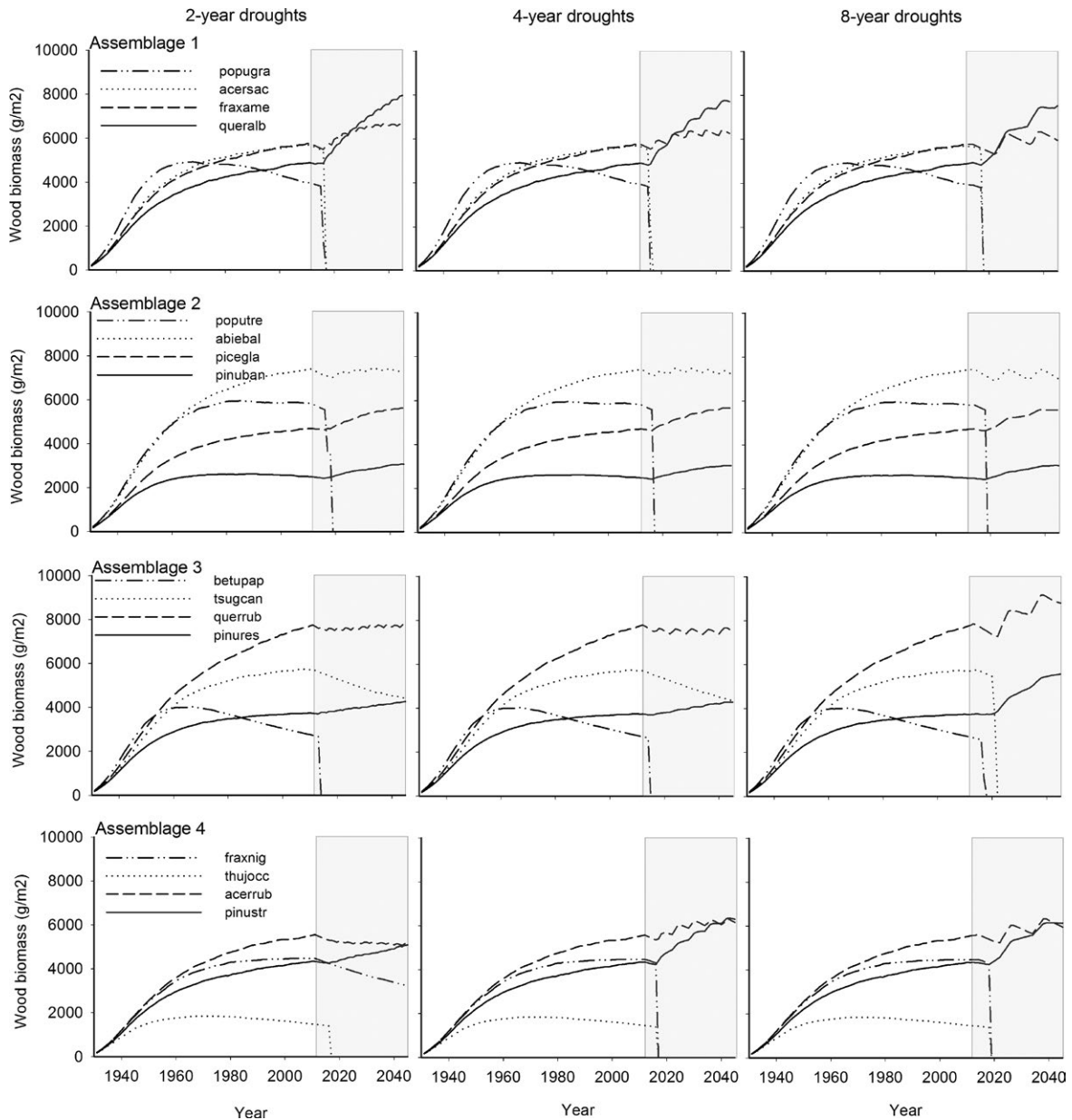
Fig. 6. Aboveground woody biomass through simulated time of Assemblages to the length of drought and soil type experimental factors on a sandy loam soil. Gray boxes indicate the period when drought treatments were applied. Cohorts died when NSCfrac <0.01 at the end of a simulation year. The mean of three replicates is shown; replicate variability is not shown for clarity.

Landscape experiment

When the species competed in many real assemblages on the nearly one million cells of the landscape experiment, the drought-induced change in total landscape biomass tended to be negative for drought-intolerant species and positive for drought-tolerant species (Fig. 8).

All species initially declined when the droughts began (year 10), presumably because many cohorts that were able to cover their maintenance costs under the no-drought spin-up period became unable to maintain their pre-drought biomass under the drought regime, and many cohorts consequently died (not shown). This
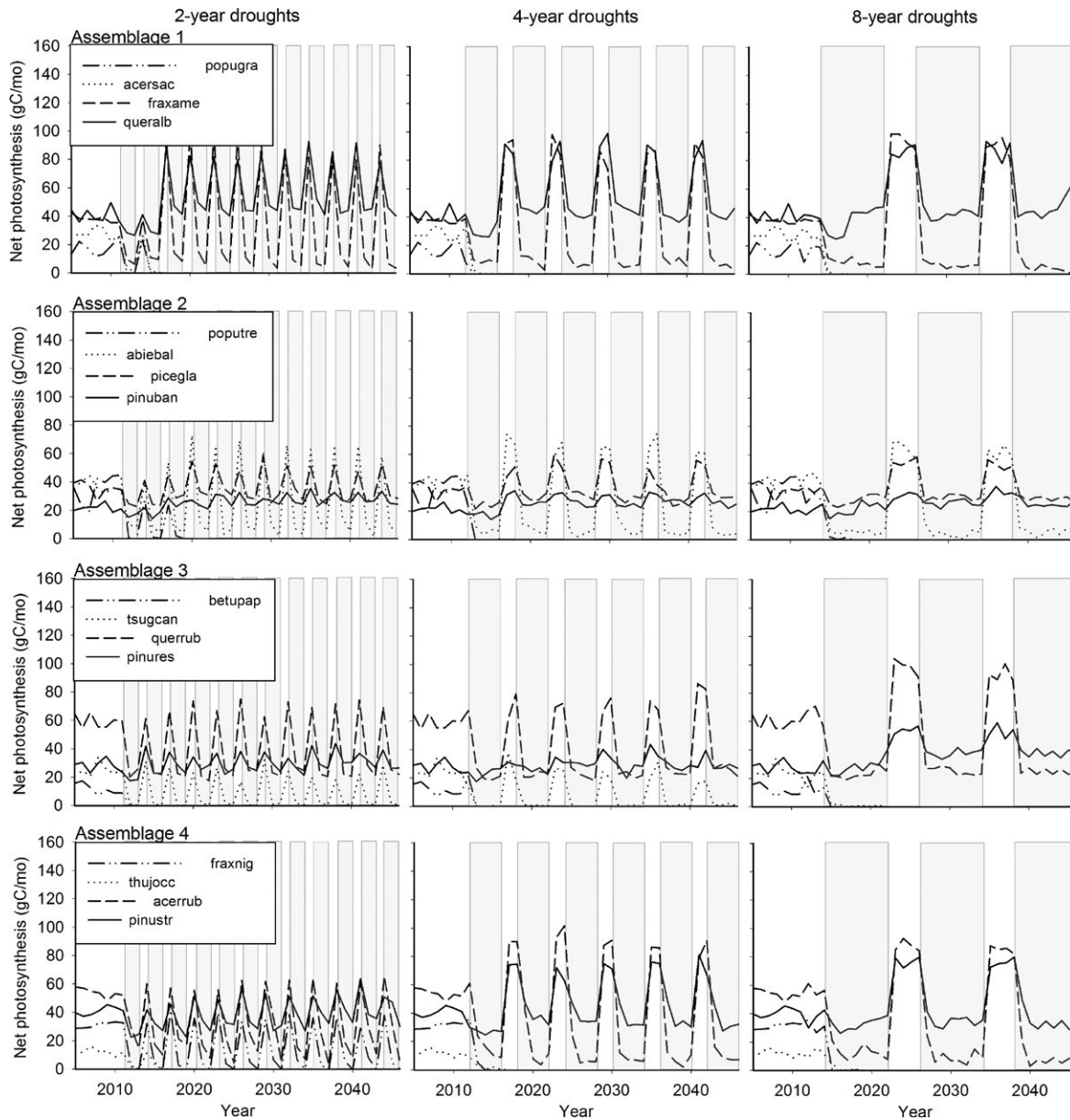
Fig. 7. Comparison of the response of net photosynthesis of Assemblages to the length of drought and soil type experimental factors on a sandy loam soil. Gray boxes indicate periods of drought. Cohorts died when NSCfrac <0.01 at the end of a simulation year. The mean of three replicates is shown; replicate variability is not shown for clarity.

was true even for drought-tolerant species, and some had lower biomass under drought than under control conditions (e.g., white pine (pinustr) and red pine (pinures)). Drought-tolerant species were generally able to regain biomass after the droughts started, while drought-intolerant species continued to decline, even

though the disturbances necessary for their persistence (they tend to be shade-intolerant) did occur. Within each drought tolerance class the species generally sorted by photosynthetic capacity (FolN) and life form (deciduous vs. evergreen), with more productive species (higher FolN) and deciduous species able to
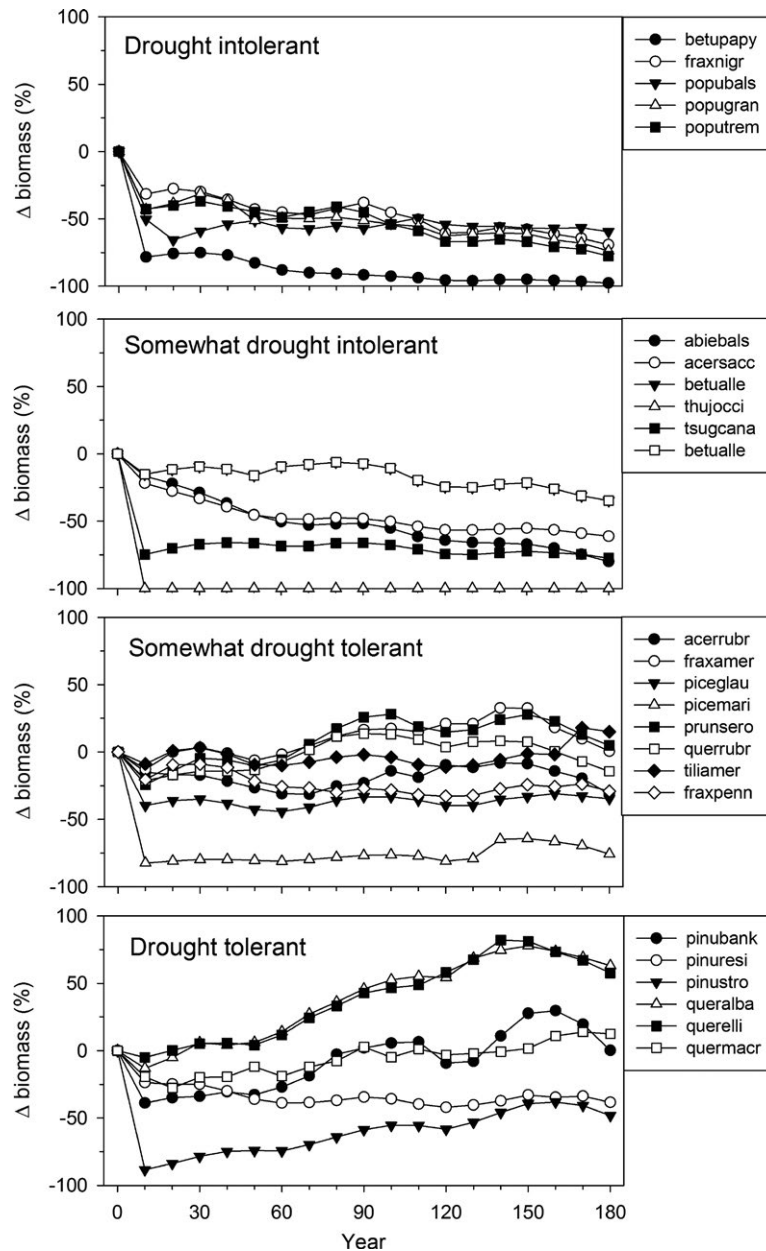
Fig. 8.   Difference in landscape-wide biomass under the drought treatment compared to the control treatment in the landscape experiment. Each symbol represents the mean of three replicates and the variability is generally less than the width of the symbols. Species not shown had extremely low biomass though time.

recover more quickly and therefore suffering less overall decline because of drought. White pine (pinustr) was the most notable exception to this tendency. It is the most highly productive conifer, yet it suffered a near total collapse when the droughts started, perhaps because of very high biomass and consequent high maintenance cost. Although it recovered 72% of its beginning biomass, it remained the least abundant drought-tolerant species after 180 yr (Fig. 8).

Soil type (ecoregion) had a marked impact on total productivity (biomass), with soils having higher PAW being more productive through time
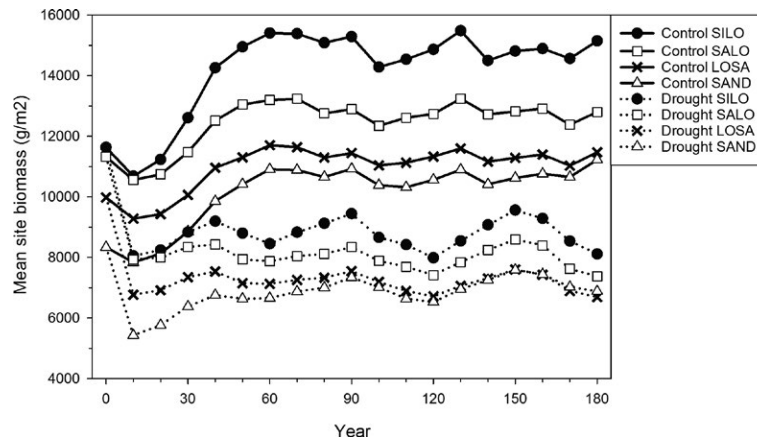
Fig. 9. Mean biomass on cells by ecoregion (soil type) and precipitation treatment in the landscape experiment. Each symbol represents the mean of three replicates and the variability is generally less than the width of the symbols.

(Fig. 9). The differences in productivity among the soil types were less under drought conditions, presumably because all soils were drained to near or below soil wilting point (−1.5 MPa). Variation in total biomass was caused primarily by the death of cohorts due to senescence, competition, or disturbance. Under the control treatment there was variability in precipitation, which affected competition for water. Under the drought treatment, precipitation cycled between normal and drought conditions on a 12-yr cycle, which is reflected in the oscillations in the biomass variable, which was output at 10-yr intervals. Note that the drop in biomass at year 10 under the control treatment was caused by a relatively dry decade in the historical weather stream.

DISCUSSION

Insights

Our overall site-level results (Figs. 3–7) clearly show that simulated NetPsn tracks drought and nondrought conditions very tightly, consistent with our expectations. Increasing drought length resulted in more instances of mortality when NetPsn became depressed too long for the cohort to be sustained by its available carbon reserves. This is consistent with the carbon starvation hypothesis (McDowell et al. 2013) on which our approach was built (see *Caveats*). NSCfrac tends to

recover quickly when precipitation returns to average levels, allowing cohorts to survive shorter droughts, although species with limited photosynthetic capability (e.g., thujocc) are less able to recover quickly. When cohorts die, simulated NetPsn of the remaining cohorts increases as the competition for available water and light is reduced (release). Initially, because water potential is likely to increase considerably with the loss of a cohort, remaining cohorts experience little water stress, but because the remaining canopy limits radiation to some extent, the more shade tolerant species (lower HalfSat) will experience less radiation stress and be better able to respond to the release (e.g., abiebal, querrub). In addition, drought that occurs following a long period of no drought (e.g., spin-up) may induce greater mortality because larger biomass pools incur greater maintenance respiration costs that reduce carbon reserves more quickly.

Our results help explain why drought-induced tree mortality is more dependent on drought length than severity as observed on forest inventory plots by Gustafson and Sturtevant (2013). Photosynthesis can be driven to zero by even moderate drought, but it cannot be driven to less than zero by more severe droughts, so severity of drought has a limited impact. Photosynthesis recovers very quickly with inputs of water, so it really is the lack of opportunity for NSC to recover as droughts lengthen that causes mortality.

In reality, cohorts that drop leaves or experience xylem damage in response to drought may be less able to recover quickly than our model suggests. Nevertheless, our results help illuminate the mechanisms behind the empirical results of Gustafson and Sturtevant (2013). They found that drought-intolerant species experience some mortality even during short droughts, and the probability of mortality rises dramatically with drought length such that the probability approached 1.0 for droughts of 8 yr (Fig. 10). Our results illustrate that these species suffer severe depression of photosynthetic rates as soon as water becomes limited, and any more drought-tolerant competitors quickly decrease water potential to the point that photosynthesis shuts down completely for the drought-intolerant species. Conversely, the most drought-tolerant species have no superior competitors for water that can drop water potential below the ability of those drought-tolerant species to access water, so they are able to continue photosynthesis enough to maintain carbon reserves for long periods of time. The sequence of mortality probability curves from drought-intolerant to tolerant in Gustafson and Sturtevant (2013) (Fig. 10) showed a declining sensitivity to drought length consistent with that observed in this study. The relative sensitivity to drought length across drought sensitivity classes was not linear (similar to Gustafson and Sturtevant (2013)), even though the distribution of H3 and H4 parameters across drought sensitivity classes was linear (Table 2), providing some confirmation that the mechanistic formulation of PnET-Succession accurately simulates reality in terms of competition for water.

The interaction of drought with tree species life-history traits, seed dispersal, and disturbance is complex. Our landscape results generally followed theoretical expectations, but each species followed a unique trajectory through time because of its unique life-history traits and the various combinations of competitors found on cells (Fig. 8). For example, species biomass did not always vary in phase, even though each experienced the same climate. There is also a possibility that drought intolerance is confounded with shade intolerance. The potential for shade-intolerant species to accumulate biomass is limited by both water and the availability of
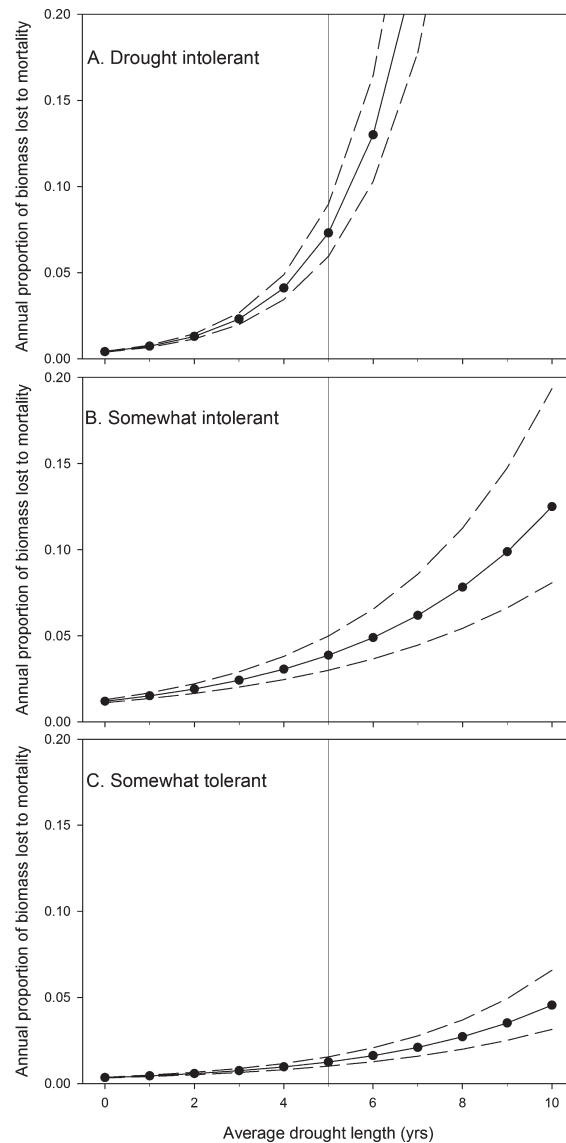

Fig. 10. Relationship between drought length and probability of biomass lost to mortality by drought tolerance class as found by Gustafson and Sturtevant (2013). No valid model was found for the drought-tolerant class, and it was assumed that drought has no effect on mortality for that class. The vertical line represents the maximum drought length used to fit the models. Reprinted with permission.

disturbed sites. In our simulations, 3.3% of the landscape was disturbed. The ability of shade-intolerant jack pine (pinuban) to increase biomass suggests that the decline of the drought-intolerant species (which are also generally

shade intolerant) is not completely due to a shortage of disturbed sites.

The injection of a first principles approach into a landscape-scale model combines the best features of stand-level models and FLMs to robustly project the impacts of global changes. Stand models are tightly linked to fundamental environmental drivers and simulate growth as a function of ecosystem inputs and fluxes, but do not simulate competition, succession or spatially explicit processes such as disturbance. Most FLMs simulate competition, succession and disturbance, but simulation of growth and competition is simplistic and not very tightly linked to environmental drivers. Our approach appears to provide advantages for simulation of landscape responses to global changes. Each species has a unique combination of life-history traits that determine its growth response to water and light availability, temperature, and CO_2 concentration, and also its varying susceptibility to multiple disturbances. These traits interact to cause a species-specific response to the fundamental drivers that are globally changing, and these species responses interact with those of competing species to create stand or ecosystem responses that are complex and difficult to accurately predict with less mechanistic approaches. Our results showing that the outcome of drought treatments can vary depending on the competing species in an assemblage illustrates the importance of using a mechanistic approach. Empirical approaches based on competitive interactions observed in the past will be less reliable in predicting the re-sorting of species into new assemblages as climate changes (Gustafson 2013).

Major assumptions

In our study we made some important assumptions. (1) Drought effects are modeled by PnET-Succession in two ways; species-specific reduction in growth caused by water limitation and a decline in carbon reserves when respiration exceeds photosynthesis. Mortality is simulated when NSC <1% of total biomass (Sevanto et al. 2013). This assumes that a carbon starvation mechanism is a reasonable surrogate for all mortality mechanisms (e.g., hydraulic failure and biotic agent mechanisms; McDowell et al. 2011), producing a similar outcome for most drought

events. This assumption remains untested and there is considerable uncertainty about the specific mechanism of death by hydraulic failure in the literature, but there is some support for the assumption (Sevanto et al. 2013, Hartmann et al. 2013, McDowell et al. 2013, Quirk et al. 2013, but see Sala et al. 2010). (2) We also assumed that NSC is a valid proxy for risk of mortality because the risk of mortality appears to increase exponentially as NSC decreases (Gustafson et al. 2015: Fig. 4). This assumption is supported conceptually by the fact that respiration cannot exceed photosynthesis indefinitely and empirically by findings that physiologically stressed trees are more susceptible to disturbance mortality (Raffa et al. 2005). Although the specific mechanisms of how and when water stress kills trees remain somewhat unclear (Sala et al. 2010), the use of NSC as a proxy for mortality risk in landscape-scale simulations is appealing because it represents a fundamental measure of the vitality of a cohort that is tightly coupled to the environmental conditions experienced by a cohort (e.g., light, water, temperature). (3) We assumed that if the mechanistic approach can adequately predict drought effects under current climate conditions, it will reliably predict future conditions because it uses mechanisms based on well-established "first principles."

Caveats

The site-level experiment attempted to mimic sites similar to those on which the FIA data were collected and used by Gustafson and Sturtevant (2013) to build the empirical relationships between length of drought and species biomass lost to mortality. We built artificial assemblages of species representing all four drought tolerance classes on each site to avoid having to duplicate the tens of thousands of FIA plots required to detect the drought signal. Some of these assemblages may only rarely occur in nature. One possible consequence of this approach is that the NSC level for a species may have at least partly been determined by the growth rate of a species relative to the others in the assemblage (i.e., competitive ability). We attempted to group species with similar growth rates, but differences nevertheless occurred, with drought-tolerant species sometimes having faster intrinsic growth than

less drought-tolerant species. However, in the real world, competitive disadvantages may be one of the factors that determine drought-induced mortality. Our experimental design did not control the effect of intrinsic growth rate, allowing species to have realistic growth rates. Also, our results do not confirm the relative drought tolerance of individual species because we assigned H3 and H4 values based on an *a priori* classification. However, our results do confirm that the H3 and H4 parameters allow PnET-Succession to mechanistically simulate relative drought effects on photosynthesis and carbon reserves. Finally, our approach does not explicitly make large cohorts (trees) more resistant to drought than smaller ones. LANDIS-II does not track size of individual trees, but it is reasonable to assume that cohorts having large biomass are likely to consist of large trees. In PnET-Succession, drought tolerance is specified by 2 parameters (H3, H4) that do not vary with the biomass of a cohort, and mortality occurs when NSCfrac <0.01. Although the target NSCfrac does not vary by cohort size, large cohorts have larger pools of NSC (better buffered) and they have higher priority access to light and water than smaller cohorts, so they are less likely to be killed by drought than are smaller cohorts on a given site.

Future work

A more mechanistic, first principles approach could be developed for many existing FLMs, especially those that simulate growth as an accumulation of biomass or volume. The addition of other mechanisms reflecting other drivers such as soil nutrients may be indicated where those drivers are changing (e.g., nitrogen deposition rates). Within LANDIS-II there is potential to pass the relative carbon reserves (NSCfrac) of cohorts to disturbance extensions, allowing disturbance (e.g., insects) to target mortality to physiologically stressed cohorts. However, research must be conducted to determine how best to coordinate the amount of direct and indirect drought-related mortality simulated by PnET-Succession and disturbance extensions, respectively. PnET-Succession currently kills cohorts when NSC levels drop below 1% of total biomass, consistent with empirical

findings (Sevanto et al. 2013, Gustafson et al. 2015), and this threshold appears to include both direct and indirect (e.g., bark beetle) mortality. An empirical basis to partition direct and indirect drought-induced mortality is needed. Furthermore, an assessment of the ability of the mechanistic approach of PnET-Succession to model the interactions of potential future combinations of temperature, precipitation, PAR (cloudiness), and CO_2 (affecting conductance and vapor pressure deficit) is now feasible.

CONCLUSIONS

We draw two main conclusions from our study. (1) The mechanistic, first principles simulation approach appears to provide advantages for simulation of landscape responses to global changes. The combination of life-history traits (including drought susceptibility) of the competitors found on a site interact to cause a site-specific dynamic response to globally changing fundamental drivers, and these site-level responses interact with those on other sites (through dispersal) and with disturbance processes to create landscape responses that are complex and difficult to predict with less mechanistic approaches. The main disadvantage of the approach is increased parameter burden and uncertainty. The nature of specific research or management questions should be used to guide the selection of an approach to balance the need for robustness to the fundamental environmental drivers that will be input to the model and the uncertainty associated with the approach. (2) Our results are consistent with the empirical findings of Gustafson and Sturtevant (2013) and suggest that the mechanism for their results is that even moderate drought severity can drive photosynthesis to zero for much of the growing season, resulting in little additional effect of more severe droughts and increasing drought length increases mortality because net photosynthesis is depressed too long for trees to be sustained by their carbon reserves.

ACKNOWLEDGMENTS

Literature Cited

Aber, J. D., S. V. Ollinger, C. A. Federer, P. B. Reich, M. L. Goulden, D. W. Kicklighter, J. M. Melillo, and R. G. Jr Lathrop. 1995. Predicting the effects of climate change on water yield and forest production in the northeastern United States. Climate Research 5:207–222.

Aber, J. D., P. B. Reich, and M. L. Goulden. 1996. Extrapolating leaf CO2 exchange to the canopy: a generalized model of forest photosynthesis compared with measurements by eddy correlation. Oecologia 106:257–265.

Aber, J. D., S. V. Ollinger, and C. T. Driscoll. 1997. Modeling nitrogen saturation in forest ecosystems in response to land use and atmospheric deposition. Ecological Modelling 101:61–78.

Abrams, M. D., and M. E. Kubiske. 1990. Leaf structural characteristics of 31 hardwood and conifer tree species in central Wisconsin: influence of light regime and shade-tolerance rank. Forest Ecology and Management 31:245–253.

Atkins, P. W. 1978. Physical Chemistry. Oxford University Press, Oxford, UK.

Bolster, K. L., J. D. Aber, and M. E. Martin. 1996. Interactions between precision and generality in the development of calibration for the determination of carbon fraction and nitrogen concentration in foliage by near infrared reflectance. Canadian Journal of Forest Research 26:590–600.

Burns, R. M., B. H. Honkala and Tech Coords. 1990. Silvics of North America: 1. Conifers; 2. Hardwoods. Agriculture Handbook 654. USDA Forest Service, Washington, DC, USA.

Chaves, M. M., J. S. Pereira, J. Moroco, M. L. Rodrigues, C. P. P. Ricardo, M. L. Osorio, I. Carvalho, T. Fabria, and C. Pinhero. 2002. How plants cope with water stress in the field: photosynthesis and growth. Annals of Botany 89:907–916.

Cuddington, K., M.-J. Fortin, L. R. Gerber, A. Hastings, A. Liebhold, M. O'Connor, and C. Ray. 2013. Process-based models are required to manage ecological systems in a changing world. Ecosphere 4:20, http://dx.doi.org/10.1890/ES12-00178.1.

Dale, V. H., et al. 2001. Climate change and forest disturbances. BioScience 51:723–734.

De Bruijn, A. M. G., R. Grote, and K. Butterbach-Bahl. 2011. An alternative modelling approach to predict emissions of N_2O and NO from forest soils. European Journal of Forest Research 130:755–773.

De Bruijn, A., E. J. Gustafson, B. R. Sturtevant, J. R. Foster, B. R. Miranda, N. I. Lichti, and D. F. Jacobs. 2014. Toward more robust projections of forest landscape dynamics under novel environmental conditions: embedding PnET within LANDIS-II. Ecological Modelling 287:44–57.

Feddes, R. A., P. J. Kowalik and H. Zaradny. 1978. Simulation of field water use and crop yield. Centre for Agricultural Publishing and Documentation, Wageningen, NL.

Franks, P., et al. 2013. Sensitivity of plants to changing atmospheric CO_2: from geological past to the next century. New Phytologist 197:1077–1094.

Gass, T. M. 2010. Plant-soil-water relations in three contrasting environments. Dissertation. Colorado State University, Fort Collins, Colorado, USA.

Gustafson, E. J. 2013. When relationships estimated in the past cannot be used to predict the future: using mechanistic models to predict landscape ecological dynamics in a changing world. Landscape Ecology 28:1429–1437.

Gustafson, E. J. 2014. Applicability of predictive models of drought-induced mortality between the Midwest and northeastern United States. Forest Science 60:327–334.

Gustafson, E. J. and A. M. G. De Bruijn. 2015. PnET-Succession v1.20: Extension User Guide. http://www.landisii.org/extensions/pnet-succession

Gustafson, E. J., and B. R. Sturtevant. 2013. Modeling forest mortality caused by drought stress: implications for climate change. Ecosystems 16:60–74.

Gustafson, E. J., Shifley, S. R., D. J. Mladenoff, H. S. He and K. K. Nimerfro. 2000. Spatial simulation of forest succession and timber harvesting using LANDIS. Canadian Journal of Forest Research 30:32–43.

Gustafson, E. J., A. M. G. De Bruijn, M. E. Kubiske, R. E. Pangle, J.-M. Limousin, N. McDowell, B. R. Sturtevant, J. Muss, and W. T. Pockman. 2015. Integrating ecophysiology and forest landscape models to better project drought effects under climate change. Global Change Biology 21:843–856.

Hartmann, H., S. Trumbore, and W. Ziegler. 2013. Lethal drought leads to reduction in nonstructural carbohydrates (NSC) in Norway spruce tree roots but not in the canopy. Functional Ecology 27:413–427.

He, H. S. 2008. Forest landscape models: definitions, characterization, and classification. Forest Ecology and Management 254:484–498.

Huston, M., and T. Smith. 1987. Plant succession: life history and competition. American Naturalist 130:168–198.

IPCC. 2013. Climate Change 2013: The Physical Science Basis. Working Group I Contribution to the Fifth Assessment Report of the Intergovernmen-

tal Panel on Climate Change. T. F. Stocker, D. Qin, G.-K. Plattner, M. Tignor, S.K. Allen, J. Boschung, A. Nauels, Y. Xia, M. Midgley, editors. Cambridge University Press, Cambridge, UK, and New York, NY, USA.

Janowiak, M. K., et al. 2014. Forest ecosystem vulnerability assessment and synthesis for northern Wisconsin and western Upper Michigan: a report from the Northwoods Climate Change Response Framework project. NRS-GTR-136. USDA Forest Service, Northern Research Station Newtown Square, Pennsylvania,USA.

Keane, R. E., R. A. Loehman and L. M. Holsinger. 2011. The FireBGCv2 landscape fire and succession model: a research simulation platform for exploring fire and vegetation dynamics. RMRS-GTR-255, USDA Forest Service, Rocky Mountain Research Station, Fort Collins, Colorado, USA.

Keane, R. E., C. Miller, E. Smithwick, D. McKenzie, D. Falk, and L. Kellogg. 2015. Representing climate, disturbance, and vegetation interactions in landscape models. Ecological Modelling 309–310:33–47.

Limousin, J.-M., C. P. Bickford, L. T. Dickman, R. E. Pangle, P. J. Hudson, A. L. Boutz, N. Gehres, J. L. Osuna, W. T. Pockman, and N. G. McDowell. 2013. Regulation and acclimation of leaf gas exchange in a piñon–juniper woodland exposed to three different precipitation regimes. Plant, Cell and Environment 36:1812–1825.

Maurer, E. P., A. W. Wood, J. C. Adam, D. P. Lettenmaier, and B. Nijssen. 2002. A long-term hydrologically-based data set of land surface fluxes and states for the conterminous United States. Journal of Climate 15:3237–3251.

McDowell, N. G., D. J. Beerling, D. D. Breshears, R. A. Fisher, K. F. Raffa, and M. Stitt. 2011. The interdependence of mechanisms underlying climate-driven vegetation mortality. Trends in Ecology and Evolution 26:523–532.

McDowell, N. G., et al. 2013. Evaluating theories of drought-induced vegetation mortality using a multimodel-experiment framework. New Phytologist 200:304–321.

Medlyn, B. E., R. A. Duursma, and M. J. B. Zeppel. 2011. Forest productivity under climate change: a checklist for evaluating model studies. Climate Change 2:332–355.

Miles, P. D. and W. B. Smith. 2009. Specific gravity and other properties of wood and bark for 156 tree species found in North America. NRS-Research Note-38, USDA Forest Service, Northern Research Station, Newtown Square, Pennsylvania, USA

Mladenoff, D. J. 2004. LANDIS and forest landscape models. Ecological Modelling 180:7–19.

Pastor, J., and W. M. Post. 1986. Influence of climate, soil moisture, and succession on forest carbon and nitrogen cycles. Biogeochemistry 2:3–27.

Quirk, J., N. G. McDowell, J. R. Leake, P. J. Hudson, and D. J. Beerling. 2013. Increased susceptibility to drought-induced mortality in *Sequoia sempervirens* (Cupressaceae) trees under Cenozoic atmospheric carbon dioxide starvation. American Journal of Botany 100:582–591.

Raffa, K. F., B. H. Aukema, N. Erbilgin, K. D. Klepzig, and K. F. Wallin. 2005. Interactions among conifer terpenoids and bark beetles across multiple levels of scale: an attempt to understand links between population patterns and physiological processes. Recent Advances in Phytochemistry 39:80–118.

Rasse, D. P., B. Longdoz, and R. Ceulemans. 2001. TRAP: a modelling approach to below-ground carbon allocation in temperate forests. Plant and Soil 229:281–293.

Reich, P. B., B. D. Kloeppel, D. S. Ellsworth, and M. B. Walters. 1995. Different photosynthesis-nitrogen relations in deciduous hardwood and evergreen coniferous species. Oecologia 104:24–30.

Richards, L. A., and L. R. Weaver. 1944. Moisture retention by some irrigated soils as related to soil moisture tension. Journal of Agricultural Research 69:215–235.

Running, S. W., and S. T. Gower. 1991. FOREST-BGC, a general model of forest ecosystem processes for regional applications, II. Dynamic carbon allocation and nitrogen budgets. Tree Physiology 9:147–160.

Ryu, S.-R., J. Chen, A. Noormets, M. K. Bresee, and S. V. Ollinger. 2008. Comparisons between PnET-Day and eddy covariance based gross ecosystem production in two Northern Wisconsin forests. Agricultural and Forest Meteorology 148:247–256.

Sala, A., F. Piper, and G. Hoch. 2010. Physiological mechanisms of drought-induced tree mortality are far from being resolved. New Phytologist 186:274–281.

Sato, H., A. Itoh, and T. Kohyama. 2007. SEIB–DGVM: a new Dynamic Global Vegetation Model using a spatially explicit individual-based approach. Ecological Modelling 200:279–307.

Saxton, K. E. and W. J. Rawls. 2004. Soil water characteristic equations.xls. http://hrsl.arsusda.gov/SPAW/SPAWDownload.html

Saxton, K. E., and W. J. Rawls. 2006. Soil water characteristic estimates by texture and organic matter for hydrologic solutions. Soil Science Society of America Journal 70:1569–1578.

Schelhaas, M. J., et al. 2004. CO2FIX V 3.1 - a model for quantifying carbon sequestration in forest ecosys-

tems ALTERRA Report no. 1068, ALTERRA. Wageningen, Netherlands.

Scheller, R. M., J. B. Domingo, B. R. Sturtevant, J. S. Williams, A. Rudy, E. J. Gustafson, and D. J. Mladenoff. 2007. Design, development, and application of LANDIS-II, a spatial landscape simulation model with flexible temporal and spatial resolution. Ecological Modelling 201:409–419.

Seidl, R., W. Rammer, R. M. Scheller, and T. A. Spies. 2012. An individual-based process model to simulate landscape-scale forest ecosystem dynamics. Ecological Modelling 231:87–100.

Serbin, S. P., A. Singh, B. E. McNeil, C. C. Kingdon, and P. A. Townsend. 2014. Spectroscopic determination of leaf morphological and biochemical traits for northern temperate and boreal tree species. Ecological Applications 24:1651–1669.

Sevanto, S., N. G. McDowell, L. T. Dickman, R. Pangle, and W. T. Pockman. 2013. How do trees die? A test of the hydraulic failure and carbon starvation hypotheses. Plant, Cell & Environment 37:153–161.

Smith, J. E., L. S. Heath, K. E. Skog and R. A. Birdsey. 2006. Methods for calculating forest ecosystem and harvested carbon with standard estimates for forest types of the United States. USDA Forest Service NE-GTR-343. Northeastern Research Station, Newtown Square, Pennsylvania, USA.

Soil Survey Staff, Natural Resources Conservation Service, United States Department of Agriculture. 2013. Soil Survey Geographic (SSURGO) Database. http://sdmdataaccess.nrcs.usda.gov/

Williams, A., et al. 2013. Temperature as a potent driver of regional forest drought stress and tree mortality. Nature Climate Change 3:292–297.

Wilson, B. T., A. J. Lister, and R. I. Riemann. 2012. A nearest-neighbor imputation approach to mapping tree species over large areas using forest inventory plots and moderate resolution raster data. Forest Ecology and Management 271:182–198.

SUPPORTING INFORMATION

Additional Supporting Information may be found online at http://onlinelibrary.wiley.com/doi/10.1002/ecs2.1253/supinfo